

PHYLETIC LINES IN THE MODERN FERNS¹

JOHN T. MICKEL²

Before we can begin to discuss the overall phyletic lines of the ferns, we must ask ourselves the rather old and trite but nevertheless crucial question, "What is a fern?" From what we know of the fossil record there were no true ferns in the Devonian, but there was a great array of now extinct groups of so-called ferns in the Carboniferous. How do we circumscribe the group, and is there any reason to question the naturalness of this taxon? Traditionally we define it as any megaphyllous plant reproducing by spores. From the great diversity of plants that we have seen placed in "the ferns" in the fossil record it seems quite possible that some groups could well have arisen separately from Devonian or Carboniferous ancestors before we would have called them true ferns. I am not proposing that we answer the question at this moment, nor am I certain that we can answer it at this point in time, but I want to keep the question open as we address ourselves to the overall view of the evolutionary lines as seen in the modern ferns.

Another major difficulty that must be mentioned before we can begin is that morphologically we are still in somewhat of a mess regarding the characters of the ferns. In an attempt to prepare an objective way of producing a phylogeny with the aid of computerization, the systematic characters of the ferns were examined rather closely. A broad comparison is extremely difficult or impossible at this time. What are the characters? We actually know little about any of them. In the first place in many cases we cannot make comparisons between the taxa. We may have information on certain characters for certain taxa, but it generally is difficult to compare the information we have between major groups of ferns. Secondly, we do not know what we are looking for in all characters. For example, in most descriptions of ferns their vestiture is described as consisting of hairs or scales and only rarely with any sort of qualifiers, such as clathrate scales or acicular hairs. In some cases the same type of scale or hair is described as being present in totally different and unrelated groups of ferns, yet no detailed study has been made to see whether in fact the two are really the same.

We have virtually no information on another aspect of vestiture, namely the paraphyses. What types are there? What is their importance to the plant? What is their phylogenetic significance? There are many other characters in just this same state of non-recognition. The work of Bower along these lines was extremely important, but the work is far from finished. We are still in the crosier stage of morphological and phylogenetic study in the ferns.

The study of phyletic lines in ferns has taken into consideration in the past virtually exclusively the modern ferns and ignored the fossil ferns. The reasons for this are good ones. The ferns of the Paleozoic are extremely diverse and

¹ Supported in part by a grant from the National Science Foundation (GB-30859X).

² The New York Botanical Garden, Bronx, New York 10458.

bizarre by modern standards with only the slightest traces of our modern groups represented in them. How they can be tied into our modern ferns is still quite up in the air (or more correctly down in the ground). The ferns suffer from the same gap that the angiosperms do, namely the fossil ferns of the Cretaceous and onward are essentially those of modern times without offering us any real assistance as to which came first or which are most primitive. Prior to the Cretaceous ferns disappear down the dark tunnel of the Jurassic and Triassic and appear on the far side in unrecognizable forms, leaving us with no guide as to the relationships and origins of our modern groups of ferns. We strongly hope that more evidence will be forthcoming from the fossil record for this time period, but for the moment we must turn our attention to the modern ferns for evidence on fern phylogeny, supplemented only sparingly with glimpses of the past.

In the past 50 years we have seen a number of phylogenetic schemes presented for the ferns. Bower's scheme (1923–28) placed great stress on the position of the sorus, marginal vs. dorsal, with only rare instances of changing from one to another, as in his "phyletic slide" found in the pteroid ferns. We now know that this does not faithfully represent all the diversity within the ferns, the shift from marginal to dorsal sori occurring several times, thus necessitating modification of Bower's tenets.

A great flush of fern phyletic fervor arose in the 1940's. Ching (1940) made a classic move in splitting the traditional Polypodiaceae into 33 families in five phylogenetic lines. The splitting itself was extreme and often ill-founded, the relationships were often based on speculation rather than solid evidence, and his five phyletic lines ended with nebulous ancestry, such as "extinct ancestral stock." In a relatively unknown paper Dickason (1946) made a plea for more solid evidence in phyletic deliberations and made a rather thoughtful analysis of the characters to be studied. Soon thereafter Holttum (1947, 1949) presented a more lengthy consideration of fern phylogeny in which he greatly recondensed the bulk of the classic Polypodiaceae into a large Dennstaedtiaceae. Although Copeland (1947) considered many relationships of the genera and families of ferns, he did not present these in a formal phylogenetic scheme.

Phylogenies have also been produced based on other grounds than strictly morphological, such as Mehra's (1961) phyletic lines based on chromosome numbers. Most recently Nayar (1970) has offered a fern phylogeny in which there has been no attempt at all to justify postulated relationships.

In the present paper I would like to present a very brief view of the modern ferns to lay out somewhat our knowledge of the relationships of the major groups, show the problems and areas of weakness in our knowledge, and propose questions that should be faced in the near future as we try to gain a clearer picture of fern phylogeny.

In this symposium Dr. Stidd has shown us in some detail the morphology of the Marattiaceae and its fossil record in the Carboniferous. In the Marattiaceae we stress especially the peculiar sorus structure (the synangium) and the stipules, large fleshy outgrowths from the leaf that often function as propagules. These stipules are often compared with those of the Osmundaceae

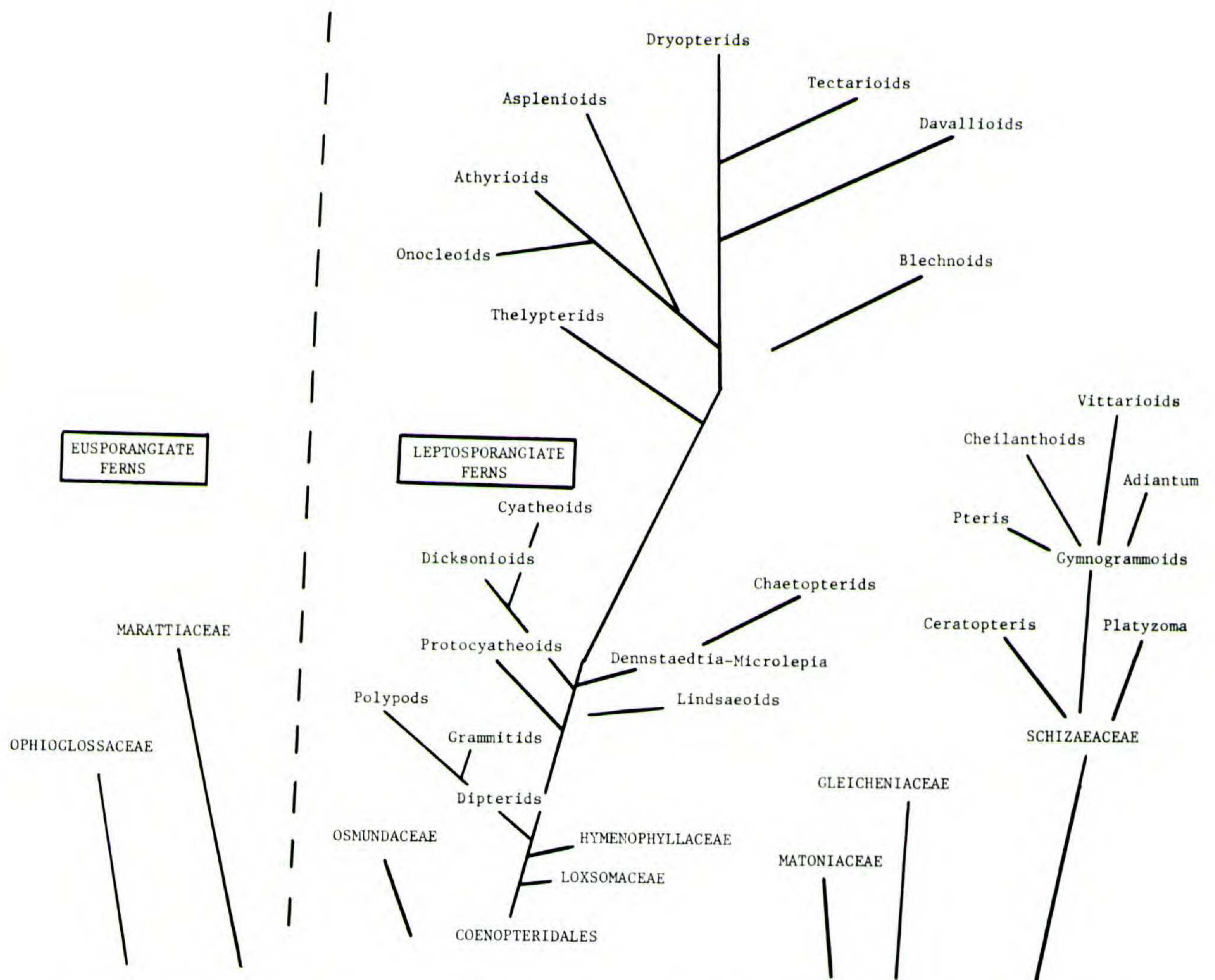


FIGURE 1. Phyletic diagram showing presumed relationships of the major groups of the Filicopsida.

and the Ophioglossaceae. A detailed comparative study would help in this matter, but it would seem that stipules in the Marattiaceae are quite different from the stipular sheaths of the Ophioglossaceae and the flared leaf bases of the Osmundaceae.

The Marattiaceae are plants that are fleshy and lack strengthening tissue. The stele is distinctive in its polycyclic dictyostele. The indument is composed of scales, but they are unlike any scales of the Filicales and are essentially amorphous. A detailed comparison of indument types in the ferns as a whole would be well worth the time. The plants contain abundant mucilage ducts, and the flesh of the plant turns pink when exposed to the air. Is this the same mucilage as in the Cyatheaceae and a few other ferns? Another feature that cements the relationships of the fossil *Psaronius* and the modern Marattiaceae is the distinct root anatomy that is common to both. Its stele contains radiating arms of xylem and phloem as opposed to the diarch protostele of virtually all other ferns.

In the Ophioglossaceae we again have soft fleshy plants without any substantial strengthening tissue. The unique features of this family include its very large sporangia, its fertile stalk of unknown origin (Is it an ancient dichotomy? Could it be a branch? Is it a fused pair of pinnae?), its subterranean

rhizome and gametophyte, and its mycorrhizal relationship in both gametophyte and sporophyte.

Quite possibly the Ophioglossaceae have an origin distinct from the rest of the ferns and probably the Marattiaceae also have arisen independently. This possibility should be given serious consideration rather than accommodating all the so-called ferns into one phyletic line and trying with great imagination to derive the characters of the leptosporangiate ferns from our modern eusporangiate representatives.

Of the leptosporangiate ferns the Osmundaceae stands part perhaps farther than most groups. It has distinct sporangia with the small lateral patch annulus, a distinctive stele recognizable in the fossil record, and is distinctly primitive in its gametophytes, sex organs, spore number and leaf anatomy. It seems to stand alone, although closer to the true ferns than to the eusporangiate ferns. Miller (1967) has given us a detailed picture of evolution within the Osmundaceae itself.

The Playiogyriaceae (*Plagiogyria*) is also distinct and primitive. For lack of any place else to put it, it is probably more closely related to the Osmundaceae than to any other group. Its pneumatophores on the petiole base are of uncertain function and origin and significance.

The main line of the ferns began with probably large leaves, marginal sori with both inner and outer indusia, creeping rhizomes, and a siphonostele. Most likely the modern protosteles are reduced from siphonostelic predecessors. Very early in the line there arose a side line with elongated receptacles. This includes the small group Loxsomaceae and the better known filmy ferns, Hymenophyllaceae. In this line the stele condition has been reduced with size to a protostele. The larger members of the Hymenophyllaceae have a distinct siphonostele.

Within the main line of the ferns we find a diversity of sporangial types, ranging from the oblique complete ring to the vertical interrupted annulus. In looking for fossil ancestors we are fortunate in having in the Coenopteridales (*e.g.* *Anachoropteris* and *Botryopteris*) a generalized type of sporangium from which any type of modern annulus can be evolved in a theoretical way.

Farther up the line we find the familiar tree ferns, basically with tall trunks, but we also find trunkless forms which are probably the more primitive. Within the tree ferns proper we have two large groups, the Dicksoniaceae, with hairs and marginal clam-like sori, and the Cyatheaceae, with an indument of scales and dorsal sori. Tryon (1970) has dealt with the latter in some detail and described the probable relationships of the subgroups of cyatheoid ferns.

At this point it becomes important to mention the diversity of stomatal types in the ferns. As has been pointed out by various authors (Kondo, 1962; Thurston, 1969; Cotthem, 1970), the stomata can be of some phyletic importance. In this symposium White has pointed out that the mature stomatal configuration cannot be used in determining the developmental type of stomate. Although this may be true in some cases, a great deal of systematic information can be gained from observation of mature stomates. Kondo (1962) pointed out the basic types of stomates, based on the number of divisions necessary to convert a stomatal initial into a stomate. Type 1 divided an epidermal cell directly into a stomate

(two guard cells), Type 2 required a division of subsidiary cell first, and Type 3 involved division to form two subsidiary cells. Basically the primitive ferns have Type 1 without any subsidiary cells, the most specialized have Type 3, and the intermediate ones have either Type 2 or a mixture of Types 2 and 3. Different types may be of diagnostic value for particular groups, but the overall trend fits any phyletic scheme, *i.e.* everyone agrees that those with Type 1 are primitive and that those with Type 3 are specialized. There is one additional type of stomate that is especially impressive in its configuration and the groups that have it. This is what Kondo called Type X. Thurston (1969) and Cotthem (1970) have pointed out the groups that have Type X. According to Bower's view (1923-28), these would fall into at least three different unrelated groups of ferns. On the contrary, it is quite possible that all are related (Mickel, 1973). There is no particular evidence to dispute this hypothesis, and it makes a great deal of sense to place them together. The groups that have Type X stomates include the dicksonioid tree ferns, the protocyatheoids (*Lophosoria* and *Metaxya*), Loxsomaceae, the dipterids (*Dipteris* and *Cheiropleuria*), and at least one primitive member of the Polypodiaceae (*Christiopteris*). Most likely the Protocyatheaceae form an independent side line not directly connected with the tree ferns. Similarly, the dipterids form another line prior to that and lead directly into the Polypodiaceae. Their stomata as well as their stele, venation, sori, and chromosome numbers support this hypothesis.

In the ferns in general venation patterns have evolved from free to netted. Within the Polypodiaceae *sens. str.*, in contrast, it is clear that the primitive condition is netted and only the more specialized groups have free veins.

In the polypod line of evolution there was an early divergence that led to the Grammitidaceae, which are distinct in their green tetrahedral spores, long hairs, and ribbon-like gametophytes. Precise relationships between the grammitids and polypods are not fully understood, and there remain a few odd genera, such as *Hyalotricha* and *Loxogramme*, whose familial dispositions are not clear-cut.

Close to the dicksonioid tree ferns are the dennstaedtioid ferns. These are characterized by their large fronds, marginal cup-like sori, creeping rhizome clothed with hairs, and often polycyclic siphonostele. In the dennstaedtioids the petiole anatomy varies greatly and can be used as a taxonomic tool. Within *Dennstaedtia* itself nearly all the species can be distinguished on the basis of the stelar configuration of the petiole (Keating, 1968). A more extended study of petiole anatomy in the ferns is needed. Keating's study was based on petiole anatomy near the base of the petiole. A more thorough study is needed to determine the value of such anatomical studies through the length of the petiole. In some cases the petiole strand may divide as it goes up the petiole, whereas in other cases it may fuse in its ascent. Just what part is the most diagnostic and in which fern groups it is helpful are yet to be determined.

Within the Dennstaedtiaceae we see another example of Bower's "phyletic slide" in which the sorus may shift from the margin to a dorsal position. We can see a morphological series from *Dennstaedtia* with its marginal sorus to *Paesia* with its reduction of the inner indusium, *Pteridium* in which the inner

indusium is nearly gone, *Hypolepis* with no inner indusium but still a marginal sorus in *H. repens* to *H. nuda* in which the sorus is in a nearly medial dorsal position.

This slide can also be seen in the closely related *Dennstaedtia* (marginal) to *Microlepia* and *Saccoloma* with the sorus moving back from the margin about a millimeter. In fact, the prime difference between *Dennstaedtia* and *Microlepia* is the sorus position, and a more complete study of this complex is needed to fully determine the generic limits.

One character that can be observed only in living material is a peculiarity in growth habit in certain members of the Dennstaedtiaceae. In *Pteridium* and some species of *Hypolepis* (Mickel, 1973) the lowest pair of pinnae may develop to maturity before the crozier will continue and produce the next pinna pair. The function and taxonomic significance of this character is not at all understood.

Another character visible generally only on living material is the branching habit of the plants. Within the dennstaedtioid ferns the branching is predominantly epipetiole; that is, the branches arise from the petiole of the leaf rather than from the stem. In some cases it is only a matter of a few millimeters out on the petiole, but it may be as much as 15 cm away from the stem. This feature is perhaps best developed and most conspicuous in *Hypolepis* in which regularly two or up to four branches develop as a major part of the stem system. Branching seems to be largely epipetiole in most of the primitive ferns of the main line of ferns. This includes the filmy ferns, dipterids, dennstaedtioids (Mickel, 1973; Troop & Mickel, 1968). This is reminiscent of the peculiar branching of *Botryopteris* and *Anachoropteris* of the Carboniferous, and whether or not there is a direct connection in evolutionary line, the consistency of the branching habit in this line of ferns is certainly significant and must be explained. It is possible that this type of branching is a remnant of branch origin of megaphylls.

Arising from the dennstaedtioids the aspidioid ferns appear to emerge, characterized by dorsal sori, bilateral spores with a well-developed perine, and a rhizome indument of scales rather than hairs. Trends in these directions are seen within the dennstaedtioids, and a good transition is seen in the genus *Monachosorum*. A great deal of diversity is seen within the aspidioid ferns, and details of their interrelationships await careful scrutiny.

The Schizaeaceae are held together largely by the sporangium with its apical annulus, which we are told by Eggert in this symposium, is not to be trusted. Within the family there are three distinct elements—*Lygodium*, *Schizaea-Actinostachys*, and *Anemia-Mohria*, each of which might possibly be considered for family rank. *Anemia* has distinct erect fertile pinnae and spores with ridges; the spores are well-known and easily recognized in the fossil record. The climbing habit of *Lygodium* and the grass-like fronds of *Schizaea* and *Actinostachys* set them apart as extremely divergent elements. The Carboniferous genus *Senftenbergia*, which has long been touted as the ancient element of the Schizaeaceae, has been found on zygopterid foliage and therefore seems to be a coenopteridalean fern. Apparently this type of sporangium has evolved more

than once and cannot be used as a definitive character for the Schizaeaceae. This does not mean necessarily that the modern members of the family are unrelated, but rather that we must use caution in ascribing schizaeaceous affinity to all fossil ferns bearing sporangia with apical annuli.

One of the most serious questions regarding the phylogenetic position of a large block of ferns involves the relationships of the Adiantaceae. Often these are placed in the main line of the ferns close to the Dennstaedtiaceae on the basis of the marginal sori in many of the genera. It seems more likely, however, that the Adiantaceae belongs closer to the Schizaeaceae. If this is so, the gymnogrammoid group of the Adiantaceae would appear to be the most primitive. They have sori that run along the veins but lack an indusium. This is much like those of *Anemia* in the Schizaeaceae, where there is no distinct sorus but the sporangia are situated on the veins. Furthermore, some of the gymnogrammoids, such as *Jamesonia* and *Eriosorus*, have hairs rather than scales on the rhizome, which is generally considered to be a primitive character. In the cheilanthoid ferns the sori are restricted more and more to near the margin, and in some the margin is differentiated and reflexed to protect the sorus. If the Adiantaceae were derived from the Dennstaedtiaceae, we would expect that somewhere there would be a remnant of the inner indusium, but there is no sign of it.

The genus *Pteris* seems to be largely a wet-forest representative of the generally xeric Adiantaceae. It differs in certain details from the rest of the group, but there is no question of its inclusion in this family.

In *Adiantum* the gymnogrammoid sorus has been restricted to an area very close to the margin, with the margin then reflexed as a false indusium; thus, the sorus is located on the underside of the false indusium. Many species of the genus have distinctive epidermal idioblasts. These idioblasts are a uniform feature of the vittarioids, which are epiphytic representatives of the Adiantaceae. The sori are gymnogrammoid in some genera, such as *Antrophyum* and *Hecistopteris*, but are linear near the margin in *Vittaria*.

The Parkeriaceae (*Ceratopteris*) is distinct in its vegetative morphology due to the aquatic habitat, but it appears to be somewhat intermediate between the Schizaeaceae and the Adiantaceae. Its spores closely resemble those of *Anemia*. The genus *Platyzoma* also shares characters of the two families, (A. Tryon 1961, 1964) and would appear to have as much right to family status as does *Ceratopteris*. It would appear to be an evolutionary offshoot with peculiar habit, anatomy, and incipient heterospory and cannot be considered part of the Adiantaceae itself.

The forking ferns, Gleicheniaceae and Matoniaceae, appear to have much in common, such as the brittle woody petioles and rhizomes, pectinate pinnae, and distinctive sori. The stele in the Gleicheniaceae is generally a vitalized protostele but is often a siphonostele. In the Matoniaceae it is a polycyclic siphonostele. The Gleicheniaceae are often credited as the ancestors of the Polypodiaceae sens. str. There is little evidence to support this view, and the stomatal evidence mentioned above is to the contrary.

The heterosporous water ferns present a major problem since we have

little to go on regarding their origin. The Salviniaceae especially has a well known fossil record, thanks to the work of Hall and his associates (Hall, 1969; Jain & Hall, 1969; Hall & Bergad, 1971; Jain, 1971). The record goes back to the Lower Cretaceous, but again disappears down the black hole of the Triassic-Jurassic. We hope that in the coming years there will appear the link to the modern or other major groups of ferns.

Finally we have purposely ignored the position of the especially difficult problem of *Psilotum* and *Stromatopteris*. Bierhorst (1968, 1969) has postulated relationships between these and has included them in the ferns. *Stromatopteris* certainly does have peculiar morphology with no clear distinction between stems, roots and leaves, and it may be related to *Psilotum*. The question, however, is whether these are in fact ferns. What is their relationship to the rest of the ferns? Are they related at all to the other ferns or did they arise independently from pre-ferns? The answers are not easy to come by.

In looking at the overall picture of the ferns, we must address ourselves to many of the questions posed here before a definitive phylogeny of the ferns will be possible. However, this does not preclude the construction of new phylogenetic schemes since these act as hypotheses and stimuli for further research. If we were to withhold our phylogenetic theorizing until all the information were available, research would be more diffuse and the final picture would be even slower in emerging. Let us use these phylogenies to help us direct our future studies on the phylogeny of the ferns.

LITERATURE CITED

- BIERHORST, D. W. 1968. On the Stromatopteridaceae (fam. nov.) and on the Psilotaceae. *Phytomorphology* 18: 232-268.
- . 1969. On *Stromatopteris* and its ill-defined organs. *Amer. Jour. Bot.* 56: 160-174.
- BOWER, F. O. 1923-1928. *The Ferns (Filicales)*. 3 Vols. Cambridge, England.
- CHING, R. C. 1940. On natural classification of the family "Polypodiaceae." *Sunyatsenia* 5: 201-268.
- COPELAND, E. B. 1947. *Genera Filicum*. New York.
- COTTHEM, W. VAN 1970. Comparative morphological study of the stomata in the Filicopsida. *Bull. Jard. Bot. État* 40: 81-239.
- DICKASON, F. G. 1946. A phylogenetic study of the ferns of Burma. *Ohio Jour. Sci.* 46: 73-108.
- HALL, J. W. 1969. Studies on fossil *Azolla*: primitive types of megaspores and massulae from the Cretaceous. *Amer. Jour. Bot.* 56: 1173-1180.
- & R. D. BERGAD. 1971. A critical study of three Cretaceous salviniaceous megaspores. *Micropaleontology* 17: 345-356.
- HOLTUM, R. E. 1947. A revised classification of the leptosporangiate ferns. *Jour. Linn. Soc., Bot.* 51: 123-158.
- . 1949. The classification of ferns. *Biol. Rev.* 24: 267-295.
- JAIN, R. K. 1971. Pre-Tertiary records of Salviniaceae. *Amer. Jour. Bot.* 58: 487-496.
- & J. W. HALL. 1969. A contribution to the early Tertiary fossil record of the Salviniaceae. *Amer. Jour. Bot.* 56: 527-539.
- KEATING, R. C. 1968. Trends of specialization in the stipe anatomy of *Dennstaedtia* and related genera. *Amer. Fern Jour.* 58: 126-140.
- KONDO, T. 1962. A contribution to the study of the fern stomata. *Res. Bull. Shizuoka Univ. Fac. Educ.* 13: 239-267.
- MEHRA, P. 1961. Cytological evolution of ferns with particular reference to Himalayan forms. *Proc. 48th Ind. Sci. Congr.* 2: 1-24.
- MICKEL, J. T. 1973. The classification and phylogenetic position of the Dennstaedtiaceae. *Jour. Linn. Soc., Bot.* In press.

- MILLER, C. N. 1967. Evolution of the fern genus *Osmunda*. Contr. Mus. Paleontol. Univ. Michigan 21: 139-203.
- NAYAR, B. K. 1970. A phylogenetic classification of the homosporous ferns. Taxon 19: 229-236.
- THURSTON, E. L. 1969. Taxonomic significance of stomatal patterns in the ferns. Amer. Fern Jour. 59: 68-79.
- TROOP, J. E. & J. T. MICKEL. 1968. Petiolar shoots in the dennstaedtioid and related ferns. Amer. Fern Jour. 58: 64-70.
- TRYON, A. F. 1961. Some new aspects of the fern *Platyzoma microphyllum*. Rhodora 63: 91-102.
- . 1964. *Platyzoma*—a Queensland fern with incipient heterospory. Amer. Jour. Bot. 51: 939-942.
- TRYON, R. M. 1970. The classification of the Cyatheaceae. Contr. Gray Herb. 200: 3-53.